

Soil Fauna on the Beech Wood Floor

Vital Role in the Balance of Nature

The woodland soil fauna is vital to the maintenance of the balance of nature. Scientists engaged in a DFG-supported project have been examining the role played by these animals in the decomposition of the carpet of leaves on the soil of the forest floor.

Although our native woods have been utilized by man for many centuries, increasing rationalisation and yield optimisation have not created such a high degree of dependence on human industrial and commercial measures as has been the case with grassland and cultivated areas. Broad-coverage spraying of pests with insecticides does, of course, take place in our spruce forests, and planta-

atmosphere and the lithosphere. The former provides oxygen, and, via water and carbon dioxide, the elements hydrogen and carbon. Moreover, the process of nitrogen fixation furnishes nitrogen. In addition to these, atmospheric precipitation produces considerable quantities of other elements, either dissolved or as aerosols. From the lithosphere, on the other hand, weathering releases mineral nutrients, chiefly alkali- and alkaline-earth,

Profile of the soil carpet in the acid-humus beech wood. The layers of this carpet have been exposed. Under the leaves of last year's fall, far left, some months old, appear first the lower litter layer, then the upper and lower fermentation layer and, right, finally, the humus layer permeated by fine roots.



tions are treated with herbicides to keep the pathways clear; but, nevertheless, in the first place, forest management is increasingly being conducted in harmony with nature, and, secondly, from the standpoint of their nutrient supply, our woods have always been, and still are, areas of vegetation which are close to nature and largely self-sufficient.

In the final analysis, the nutrients supplied to a near-natural terrestrial ecosystem originate from two sources: the

and other metals. Unlike the areas which are under intensive farming, it is the internal nutrient cycle in the woods and forests which plays the dominant role. The annual shedding of the leaves alone enables a considerable portion of the plant mass formed by primary production to reach the soil, and, in addition to this, even where woodlands are subject to commercial exploitation, a large part of the nutrients bound up in the wood remain within their confines. Thus the recycling of the nu-

trients from dead wood and leaves in a form available to plant-life becomes of vital significance for the maintenance of material and energy levels in woodland. As autotrophic plants take their nutrients in mineral form, the goal of rotting vegetation is to produce remineralisation.

The biological processes in the soil which effect this decomposition are extraordinarily complex and a first description can only be in a very simplified form. The main vehicles of disintegration are two groups of organisms: the microflora, which comprises mainly bacteria and fungi, and the soil fauna, which embraces a broad spectrum of species extending over the whole animal kingdom from protozoa to vertebrates. It is the role of this soil fauna in the decomposition of these fallen leaves which is the actual topic of our research project, and an acid-humus beech wood growing on the middle red sandstone of the northern foothills of the Black Forest near Ettlingen which is the scene of our investigations.

The mature stand of beeches (*Fagus sylvatica*) interspersed with odd durmast oak trees (*Quercus petraea*) provides an unbroken (crown) canopy which prevents any layer of shrubs or weeds from developing beneath it. The soil, an oligotrophic brown earth, supports a carpet of fallen leaves formed into three distinct layers.

If test plots are covered by coarse-mesh netting, each annual fall of leaves can be analysed separately year by year. Taken from top to bottom, the arrangement of the different layers then provides a clear picture of the nature and pace of disintegration, which can subsequently be documented macroscopically, gravimetrically and using the most diverse chemical analyses.

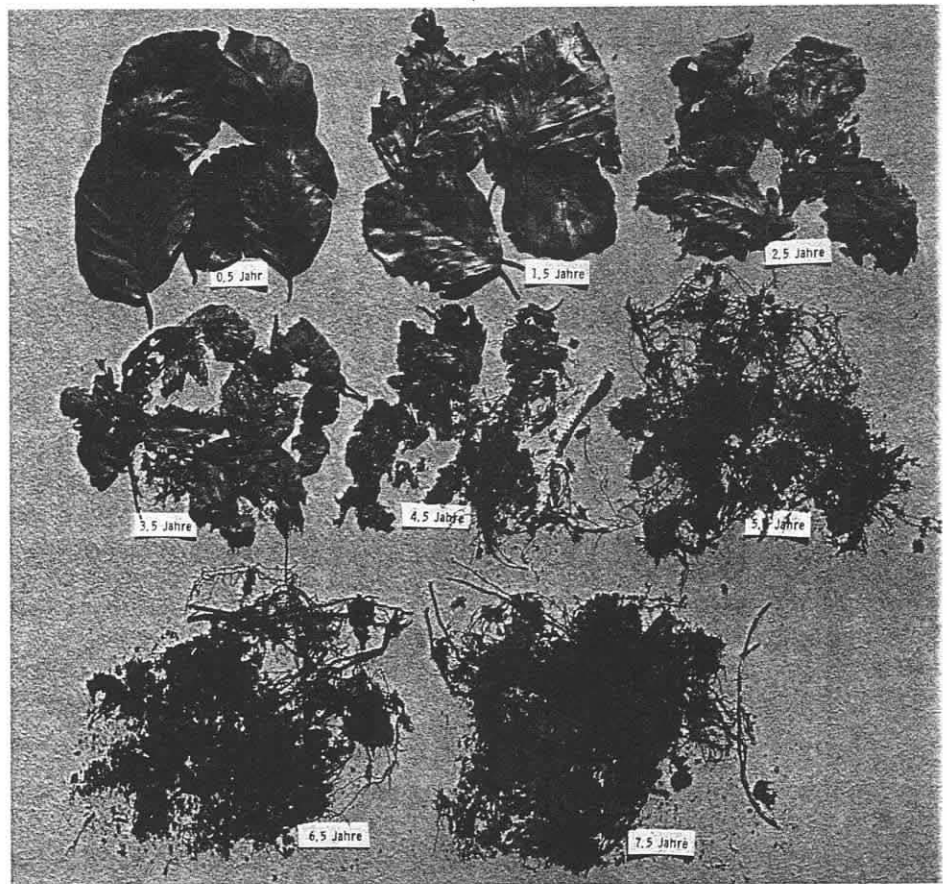
Macroscopically speaking, the sequence of decomposition of the individual years' fallen leaves takes the following form: the newly fallen leaves undergo practically no change in the first year: they are constantly being blown around by the wind and dried out, thus providing very unfavourable conditions for attack by saprophagous primary decampour organisms. These, however, soon get to work when, after one year, the leaves are subsequently covered by those of the following

year's fall and the action of winter moisture, and particularly of snow, flattens them into the soil. Discolouration indicates colonisation by microflora, especially fungi, and as the second summer approaches there are also indications that animals have been eating the leaves; the leaves now pass from the litter layer into the fermentation layer. It is here that structural disintegration reaches its peak through the activities of a multitude of soil organisms. It takes three and a half to four years for the leaves to pass through this fermenta-

tion layer; but, at the end of the "passage" the leaves as such have disappeared to become transformed into fragments of leaf ribs, only the more resistant elements such as twigs and pericarps being still recognisable. After five or six years, that year's fallen leaves, now macroscopically almost completely decomposed, land in the humus layer where the humus substances they have produced already collect and, in the course of an unknown number of years, sink further and further into the ground, mingling with the

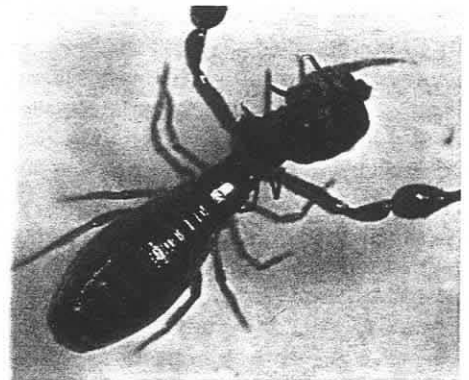
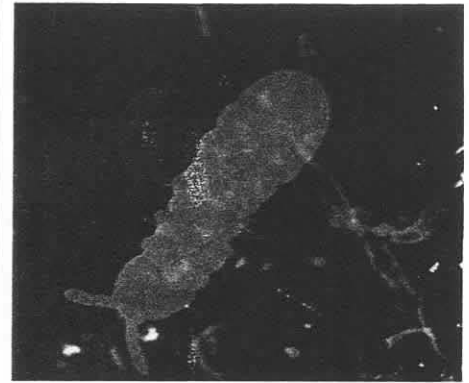
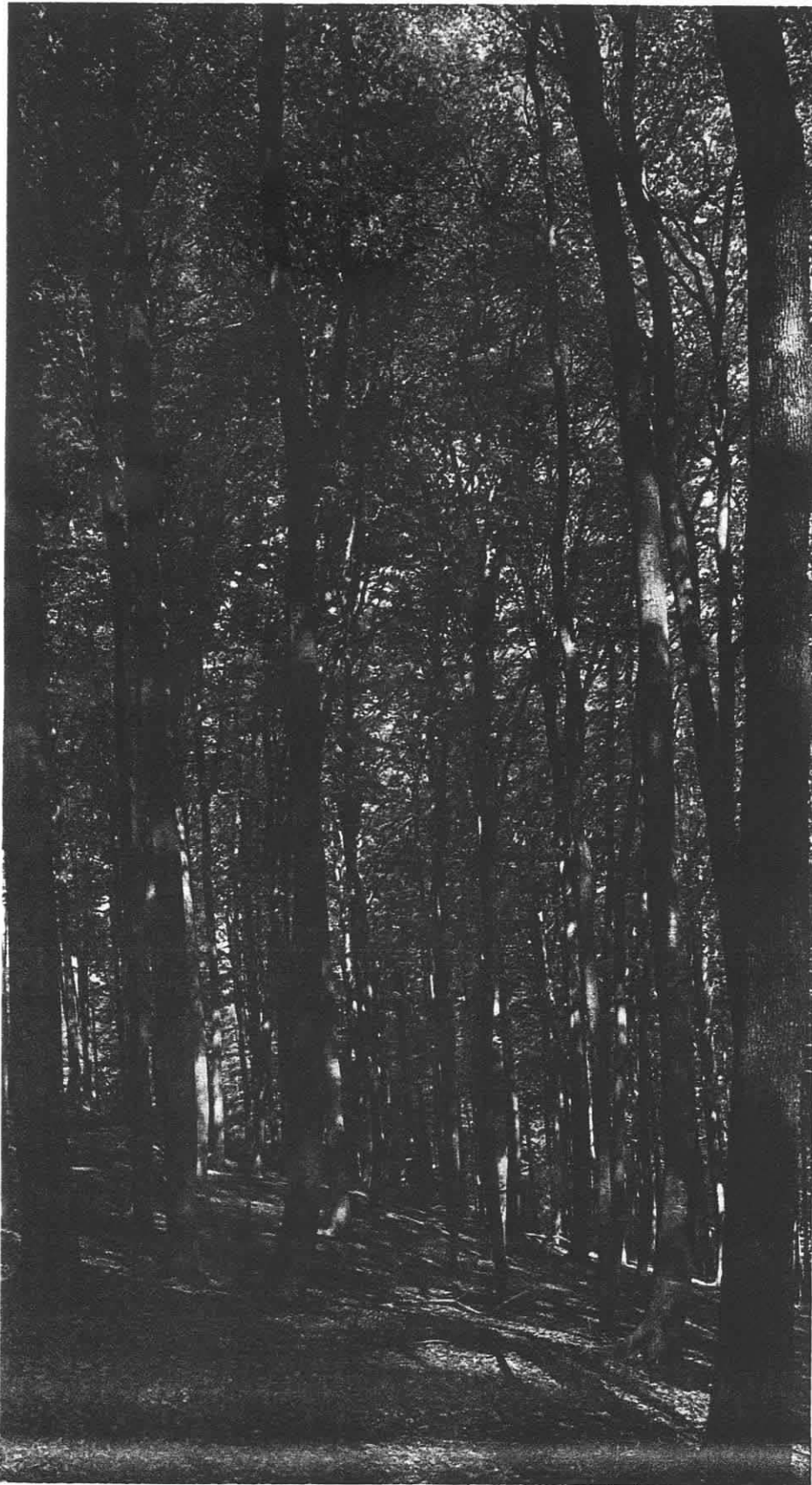
weathering detritus and minerals of the original rock or, in the case of our beech wood, with the quartz sand of the red sandstone. Simultaneously, the products of decay which are not converted to humus become completely mineralised and, balanced between adsorption to the humus particles, dissolving into the soil and absorption by roots, they remain for the most part stored in the layer of humus.

Chemical analysis permits the course of decomposition described above to be reconstructed. Thus, for example, the ni-



Stages of decomposition of dead leaves in an acid-humus beech wood starting in the top row with leaves from the previous year's fall, a few months old, to 5½-year-old leaves in the middle layer of disintegration containing macroscopically scarcely recognisable leaf residues already permeated by fine roots. The bottom row shows two years' falls 6½ and 7½ years old.

trogen content almost doubles in the first two years after the leaves have fallen, only to decline gradually as the leaves pass through the fermentation layer and, as they pass into the humus layer, it falls off rapid-



Left: The beech wood of the study area; above: Springtail (collembolous), below: A pseudoscorpion which feeds on collembolous.

ly. The carbon/nitrogen ration which is often used to indicate the biological utility of plant material, sinks correspondingly from an unfavourable initial figure of between 50 and 60, to around 30, which is maintained during the main phase of decomposition in the fermentation layer, only regaining its initial value in the humus layer.

One important element, not only as a macronutrient but also as an indicator in the soil profile, is calcium. The original rock, the red sandstone, contains almost no calcium. The calcium, in fact, is bound to the organic bed of leaves where it is enriched, especially in the form of calcium oxalate, by soil fungi. Fungoid hyphae achieve calcium contents of 8% of their dry mass, whereas fallen leaves only contain 0.4–0.6% calcium. Hence the calcium content of a leaf sample can be used as a measure of its degree of colonisation by fungi.

Once the easily soluble substances such as sugars have been washed out of the fallen leaves at the start, the first step in

their disintegration takes place when the macromolecular basic material of the discarded vegetable matter, primarily lignin and celluloses, are split up into fragments of lower molecular weight. The enzymes required for this process are supplied by the saprophagous primary decomposers, whereby many soil organisms make use of symbiotic bacteria, yeasts and protozoa. As primary decomposers, these soil animals are in competition with soil fungi, which, just where the disintegration of lignin and cellulose is concerned, play a major role. This competition is governed by the environmental conditions. In a calcareous beech wood, where the substrate is neutral to slightly acid, the large soil animals such as earthworms, snails, diplopods and wood lice predominate and initiate rapid decomposition, which results in an optimum mull humus. The more acid the environment becomes, the more prominent become the fungi, and even at a pH-value of around 4, such as we have in our acid-humus beech wood, decomposition slows down and starts taking the direction of mildew and raw humus, where only smaller forms of organism such as dipterous larvae, enchytraeids and certain species of moss mite and collembola compete with the fungi as primary decomposers.

Only a small portion of the vegetation devoured is actually utilized by these primary decomposers themselves, the major portion being excreted in a form which is now both mechanically and chemically better disintegrated; these faeces provide the staple diet for coprophagous secondary decomposers. The majority of these, however, have specialised themselves on the numerous soil fungi, which provide food for them rich in both energy and nutrients. These fungi-eating, or mycophagous, organisms are of vital significance in the acid-humus beech wood: grazing by the fungoid flora intensifies the growth of hyphae, thus optimising the process of decomposition.

This can be demonstrated by a field experiment. Freshly fallen leaves are placed into mesh-bags of varying mesh size: the finest only permits microflora and microfauna, essentially protozoa and most

nematodes, to enter; the medium-sized mesh excludes the macrofauna, whereas the coarse mesh accepts all the soil organisms. The bags are laid out in the test area and every two months two of them are removed and examined. It emerges that during the first year the calcium content of the fine mesh rises rapidly, attains its maximum after one year and remains at this level, whereas in the medium and coarse mesh bags it rises much more slowly, declines after one year and by the end of two years it has sunk to $\frac{1}{3}$ that of the fine mesh bag. If the calcium content is taken as a measure of fungus colonisation, then this finding may be interpreted as resulting from the fungi grazing through the soil fauna which, of course, except for the microfauna, only entered the bags through the medium and coarse meshes. As the differentiation of the fauna between the coarse and medium meshes reveals, if the macrofauna are excluded, a doubling of the mesofauna, chiefly moss mites and collembola, is sufficient to replace the total activity of all the mycophagous organisms. This optimisation of the process of disintegration is clearly revealed by the fact that after two years the total weight loss of the fallen leaves in the coarse and medium meshes was around 70% of the original figure, whereas in the case of the fine mesh it was only 30–35%.

Predators significant for Soil Fauna Control

The saprophagous, coprophagous and mycophagous fauna, in their turn, also form a staple diet for numerous predators, such as spiders, pseudo-scorpions, centipedes and beetles. The numbers of different species identified – 96 spiders, 22 ground beetles (carabids), 91 rove beetles (staphylinids) – alone are enough to underscore the significance of these predators in soil fauna control.

In the first phase of disintegration, the enzymatic decomposition of the initial material of this discarded vegetation produces fragments of low molecular weight which undergo a variety of subsequent processes. One part is "burnt up" by the

microfauna and soil fauna to meet their own energy requirements; but their primary task is to act as raw material and as sources of energy for complete remineralisation, and thus for conversion into an anorganic form which can be utilized by plantlife. This second stage of disintegration is almost solely the work of bacteria which, like the saprophagous fungi, are controlled by the soil fauna. It is here that the main field of activity of the microfauna, and especially of the numerous protozoa and nematode species, must lie.

A certain proportion of the reactive fragments from the first phase of disintegration, chiefly the aromatic oligomers of the lignins, condense to humus substances and thus form a new store of relatively resistant high-molecular substances which are subject to delayed mineralisation.

The soil fauna is thus involved in the biological processes of two food networks, the first of which is initiated by saprophagous organisms, primarily soil fungi, whereas the second is based on the mineralisers, the bacteria. The functions of the soil fauna in these food networks can be characterised by three trophic levels: primary decomposers, secondary decomposers and predators, although this is a gross oversimplification of the multitude of forms of diet involved.

The total number of species of soil fauna in our acid-humus beech wood in all three trophic *stages* is estimated at between 200–400 each – no doubt a surprisingly large number for a habitat such as the soil of a beech wood, which would appear at first sight to be so uniform in structure. Each of these species has its own characteristic diet and thus its own place in the biological processes occurring in the soil. However, it is obvious that where such large numbers of species exist the "ecological niches" of the individual species overlap to a great extent, and that this multiple covering of functions, this "ecological redundancy", must provide the main explanation for the self-regulatory capacity of the soil as a habitat.

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